NEW YORK ENTOMOLOGICAL SOCIETY
LXXXIX(3), 1981, pp. 152–157

PREPUPATION BEHAVIOR AND PUPATION OF THE PREDACEOUS DIVING BEETLE *DYTISCUS VERTICALIS* SAY (COLEOPTERA: DYTISCIDAE)

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Abstract.—Preceding pupation, *Dytiscus verticalis* larvae burrow into soil above the waterline. They construct pupal cells using mandibles, legs, and body wriggling. Pupal cells are nearly spherical and the openings are sealed from the inside with soil placed there by mandibles. Beetles spent 20 to 34 days in pupal cells. Newly eclosed adults are white but darken in 8 to 14 h. Pupae are described.

Introduction

Information concerning prepupation behavior and pupal stages of North American Dytiscidae is either lacking or fragmentary. In his review of dytiscid biology, Bertrand (1972) presented descriptions of larvae and pupae of some species. Matheson (1914), Wilson (1923), and Leech and Chandler (1956) have presented accounts of dytiscids which form pupal cells by burrowing into mud. James (1969) described eggs, larvae, and pupae of five species of dytiscids, all of which apparently construct pupal cells in mud along pond margins. However, actual construction of a pupal cell was only observed for one species, *Acilius semisulcatus* Aube (James 1969).

Dytiscus verticalis occur in shallow, weedy, temporary and permanent ponds in woodlands and open fields. The larva was described by Wilson (1923) but the pupa is undescribed.

This paper describes pupal cell construction behavior, pupal cells, pupal stages, length of pupation, and length of time to full coloration for *Dytiscus verticalis* reared under laboratory conditions.

Methods

Two hundred and fifty-six *D. verticalis* larvae were collected from four ponds on or near the E. N. Huyck Preserve, Rensselaerville, N.Y.; 50 of these were used in the lab rearing study. Observations from two pupae found along margins of two of these ponds are also included. Larvae were held in circular plastic chambers 15 cm in diameter, 6.5 cm in depth, and contained 4 to 5 cm of water. Each larva was fed several frog tadpoles (*Rana, Hyla*) and/or salamander larvae (*Ambystoma*) daily.

Beetle larvae which appeared ready to pupate (ceased feeding, became lethargic, and did not strike at prey) were measured by displacement volume

(this method was used to minimize the risk of injury during handling, Brodie et al. 1978) and transferred into water of one of the three types of chambers described below.

(a) 10 gal. glass aquaria (26 × 51 cm).—These chambers had a maximum soil depth of 15–20 cm, a soil slope 30 cm long (approx. 30°), and water added at one end to a depth of 3 to 4 cm.

(b) 20 gal. glass aquaria (30 × 76 cm).—The slope was 60 cm long (approx. 20°), maximum soil depth was 11 cm, and water depth was 5 cm.

(c) Circular plastic chambers (15 cm diameter).—These chambers contained no standing water but had a level layer of moist soil 4.5 cm deep.

Behavior of each larva was observed continuously for two hours after introduction into one of the chambers. For descriptive purposes representative pupae were uncovered and preserved at 7 and 14 days (4 and 1 respectively) after the larval skin was shed. Length of pupation and time from eclosion to attainment of adult coloration were recorded. Dimensions of some pupal cells were measured after the adult had left or was removed. Pupal cells of two field collected pupae were also measured and the pupae immediately preserved. Newly eclosed and fully colored beetles were sexed and preserved.

Results

A) Pupal cell construction.—Five categories of behavior were sequentially involved in the construction of a pupal cell after the beetle crawled onto the soil. 1) The initial hole was dug by moving mud pellets with scooping motions of the legs and pushing motions of the head (observed in 21 larvae). This hole was usually as wide as the larva and at least one-half its length deep. 2) Eleven larvae were observed to push their bodies head first into this initial hole which they widened and deepened by body wriggling. 3) During the widening process described above, 12 beetle larvae were observed to move pellets of mud out of the hole by grasping them with their mandibles. 4) Mud pellet grasping was used by 12 larvae to form the pupal cell into a roughly spherical shape. 5) Finally, 12 larvae closed the cell from the inside by placing pieces of mud in the hole with the mandibles.

Pupal cell construction was completed in 20 min to 12 h. Variability in amount of time needed to complete a pupal cell may have been the result of differences in soil texture or moistness within the chambers. The size of the *Dytiscus* larvae placed into chambers to pupate varied from 1.4 to 2.0 cc ($\bar{x}$ = 1.79 cc).

Mean vertical diameter of pupal cells in the lab was 35 mm and mean horizontal diameter 36 mm. Pupal cells found in the field were 26 × 35 mm and 28 × 32 mm. Cells in chambers a and b were located from 220 to 590 mm ($\bar{x}$ = 338 mm) upslope from the water at soil depths of 64 to 110 mm

Table 1. Description of 5 pupae, 7 (a, b, c, d) and 14 (e) days after shed of the larval skin.

	Pupa				
	a	b	c	d	e
Total length (mm)	31	35	36	37	36
Max. width (mm)	12	15	9	13	16
Setae number					
Head	60	47	53	43	62
Pronotum	148	134	144	131	141
Mesonotum	9-M-9	9-M-7	7-M-6	6-M-6	8-M-7
Metanotum	6-M-6	5-M-6	6-M-5	7-M-6	6-M-7
Abdominal segments					
1	7-M-7	6-M-8	7-M-7	5-M-6	6-M-6
2	9-M-10	10-M-9	9-M-10	8-M-7	7-M-6
3	10-M-8	10-M-6	9-M-8	6-M-8	8-M-7
4	8-M-9	9-M-6	9-M-9	7-M-8	10-M-9
5	8-M-7	9-M-9	8-M-9	6-M-6	8-M-9
6	8-M-8	9-M-7	8-M-8	6-M-5	9-M-8
7	17-M-18	20-M-14	16-M-13	17-M-14	19-M-12
8	26-M-26	29-M-25	27-M-33	27-M-24	25-M-30
Sex	♂	♀	♀	♂	♀

($\bar{x}$ = 89 mm). The floor of three pupal cells was below the waterline and one of these three pupae successfully eclosed. There were 44% males and 56% females among the successfully reared beetles. There were no consistent differences between the three types of chambers in the parameters that were measured.

B) Description of pupa.—The following description is based on the combined observations on two male and two female 7-day pupae and one female 14-day pupa (Table 1).

Measurements of lab reared pupae: length—31 to 37 mm ($\bar{x}$ = 34.8 mm); maximum width—9 to 16 mm ($\bar{x}$ = 12.3 mm). Measurements of field collected pupae: length—32 to 36 mm; maximum widths—11 to 14 mm. Caudal cerci 2 mm long in all pupae.

Head setae arranged as follows ($\bar{x}$ = 50.8): 14 to 18 along continuous anterior curve between eyes; 1 to 3 at inner posterior corner of each eye; 2 to 3 in each of two groups ventromedial to each eye; and 21 to 32 across posterior margin of head.

Pronotum with 131 to 148 setae along the lateral, posterolateral, and anterior margins and along disc. Setae on mesonotum, metanotum, and eight abdominal segments variable and unequal on opposite halves of pupae (see Table 1) (formula used to indicate number of setae on left and right halves of each pupa is from Spangler (1973), midline is indicated by—M—between

Fig. 1. Newly eclosed adult *Dytiscus verticalis* in pupal cell.

the numbers). Ninth abdominal segment terminates in two cylindrical cerci, each bearing 40 to 50 setae. One pair of spiracles on first six abdominal segments, located on each anterolateral corner.

Antennae directed ventrally underneath head, between the wing pads and the femora. Tibiae of first two pair of legs folded against femora with tarsi

parallel to body axis. Metafemur and metatibia under hind wing pads and not folded; metafemora are directed away from the tibia toward the midline.

Dorsal setae associated with thick spine-like projections which are largest along midline of fifth abdominal segment.

C) Coloration.—Immediately after shedding larval skin (7 days after cell construction), pupa was white but changed to yellowish-white within a few hours. Legs, antennae, and mouth parts darken 7 days after eclosion. Pupae light brown with dark brown appendages just prior to eclosion. Length of time in pupal cell varied from 20 to 34 days ($\bar{x}$ = 24.9 days).

Newly emerged adults were white (Fig. 1). Wing covers expanded to cover the abdomen within five minutes of eclosion and were white with longitudinal brown streaks. Eyes and tip of abdomen were dark brown. Adult pigmentation developed dorsally and ventrally from posterior to anterior in a V-shaped pattern and took from 8 to 14 h ($\bar{x}$ = 10.5 h). Beetles remained in pupal cells throughout this process. Subsequent period of time spent in pupal cells was not determined. Fully colored adults were transferred to circular plastic chambers (half filled with water and half with soil). All newly eclosed adults fed within 24 h of eclosion (0.2 cc *Hyla* tadpoles).

Discussion

Dytiscus verticalis has a larger pupal cell and a longer pupation period than either *D. fasciventris* Say or *Acilius semisulcatus* which James (1969) described. This is probably because *D. verticalis* is larger in all life stages than either *A. semisulcatus* or *D. fasciventris*. *Acilius semisulcatus* also exhibits at least one of the categories of pupal cell construction behavior that we observed in *D. verticalis*. James (1969) described soil grasping using the mandibles by *A. semisulcatus* during pupal cell construction.

There was no apparent difference in pupal cells between lab reared and field collected *D. verticalis* pupae. However, eclosion success of beetle larvae which had constructed cells in the lab (50%) may have been different than under field conditions. Other factors such as drying and predation (one field collected pupae found by us had been killed by ants) may lower eclosion success in natural situations.

Acknowledgments

This study was conducted while the authors were supported by NSF-DEB78-11196 and the E. N. Huyck Preserve; we thank R. C. Dagleish, Executive Director, for courtesies extended and help in the research. Student members of Earth Watch helped collect and observe beetles. We thank P. J. Spangler of the Smithsonian Institution for his identification of the beetles. We also thank M. S. Bobka and J. C. Bodenwiser for their comments on the manuscript.

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Received for publication September 4, 1980.